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NOTES ON THE NATURAL HISTORY OF THE LITTLE-KNOWN ECUADORIAN HORNED ANOLE, *ANOLIS PROBOSCIS*

JONATHAN B. LOSOS[1,2,3], MELISSA L. WOOLLEY[1], D. LUKE MAHLER[1,2,8],
OMAR TORRES-CARVAJAL[4], KRISTEN E. CRANDELL[5], ERIC W. SCHAAD[6], ANDREA E. NARVÁEZ[4],
FERNANDO AYALA-VARELA[4], AND ANTHONY HERREL[7]

ABSTRACT. Until very recently, the horned anole of Ecuador, *Anolis proboscis*, was known from only six male specimens, the last collected in 1966. The species was rediscovered in 2005 and in subsequent years additional specimens have been collected in the general vicinity of the type locality. These include several females, which lack the conspicuous rostral appendage seen in males. Despite rediscovery, the natural history of this enigmatic anole remains almost completely unknown. We conducted an ecological and behavioral study of this species near Mindo, Ecuador. *Anolis proboscis* is an extremely slow-moving and cryptic species that often occurs high in the trees. The rostral horn notwithstanding, *A. proboscis* is indistinguishable from Greater Antillean anoles of the "twig" ecomorph class in morphology, ecology, and behavior. The possession of a horn only by males suggests a role in sexual selection. We found the horn in life to be soft and highly flexible and thus unsuitable for use as a weapon in male–male combat; hence, the horn most likely serves as a signal and may be involved in mate choice or territorial displays. However, we did not observe any social encounters during our observations and are thus unable to test these hypotheses. Given its cryptic morphology and behavior, it is not surprising that *A. proboscis* is so rarely observed.

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[1] Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, U.S.A.

[2] Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, U.S.A.

[3] e-mail: jlosos@oeb.harvard.edu.

[4] Escuela de Biología, Pontificia Universidad Católica del Ecuador, Avenida 12 de Octubre y Roca, Apartado 17-01-2184, Quito, Ecuador.

[5] Field Research Station at Fort Missoula, Division of Biological Sciences, University of Montana, Missoula, Montana 59812, U.S.A.

[6] Department of Biology, MSC03 2020, University of New Mexico, Albuquerque, New Mexico 87131, U.S.A.

[7] UMR 7179 Centre National de la Recherche Scientifique/Museum National d'Histoire Naturelle, Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France.

[8] Present address: Center for Population Biology, 2320 Storer Hall, University of California, Davis, One Shields Avenue, Davis, CA 95616, U.S.A.

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INTRODUCTION

Among the legions of little-known anoles, one small group stands out for its combination of unusual morphology and complete absence of natural history information. The *Anolis laevis* species group (Williams, 1979) contains three putatively closely related species that bear an appendage of varying size on the tip of their snout. These three species have rarely been collected. *Anolis laevis* from Peru has not been seen since it was described by Cope in 1876 on the basis of a single preserved male specimen. The Brazilian species *A. phyllorhinus* was known from only two male specimens until fieldwork in the Amazon a decade ago led to the capture of eight specimens, including a female (Rodrigues *et al.*, 2002). The third species, the Ecuadorian *A. proboscis*, was also an enigma until recently. Known for decades from only six specimens, all male and last collected in 1966, nearly four decades passed without a reported sighting until 2005, when ecotourists on a bird-watching trip discovered one crossing a road near the type locality (Almendáriz and Vogt, 2007; C. Vogt, personal communication). Subsequently, five more specimens, including the first females, were located in two new areas in 2007 and 2008, extending the species' known distribution 11–13 km northward (Yánez-Muñoz *et al.*, 2010). Eleven more specimens were found near the type locality in 2008 and 2009 (Poe *et al.*, 2012).

Little is known about the natural history of these species as well. The recent Brazilian expedition presented habitat data for nine specimens of *A. phyllorhinus*, indicating that they occur at varying heights on medium- to large-diameter trees; once observed, most lizards moved higher into the tree. Rodrigues *et al.* (2002, pp. 374–376) concluded: "Sample size is too small to indicate microhabitat perch preference, but it appears that *A. phyllorhinus* explores virtually all structural habitats on the trunk of thin to thick trees from the ground level to the canopy. Although most specimens were first sighted at low heights in trees, they climbed quickly when disturbed, jumping eventually on to branches and leaves."

Even less is recorded about the natural history of *A. proboscis*. In addition to the road-crossing male described above, Yánez-Muñoz *et al.* (2010) reported capturing two females during the day in small bushes and Poe *et al.* (2012) collected sleeping individuals from twigs at heights of 2–9 m above the ground.

A primary question of interest with these lizards concerns the use of their rostral appendage, which we will henceforth refer to as a horn, leading to the name "horned anoles" for the group as a whole. Before Rodrigues *et al.* (2002), only male horned anoles were known, but these workers discovered that the horn was absent in female *A. phyllorhinus*, a finding subsequently mirrored in *A. proboscis* (Fig. 1; Yánez-Muñoz *et al.*, 2010; Poe *et al.*, 2012). This dimorphism suggests a role for the horn in sexual selection, but in the absence of data on the behavior and ecology of these species, this hypothesis cannot be tested.

More generally, information on the natural history of these species is important in understanding the evolutionary diversification of *Anolis*. Anoles in the Greater Antilles are renowned for repeated divergent adaptation into multiple different kinds of habitat specialist. On each island in the Greater Antilles, species have diverged to occupy different ecological niches, adapting, for example, to use grassy habitats, twigs, and tree canopies. Most remarkably, similar sets of habitat specialists, termed ecomorphs, have evolved independently on each island in the Greater Antilles (Williams, 1972, 1983; Losos, 2009). In contrast, despite the great

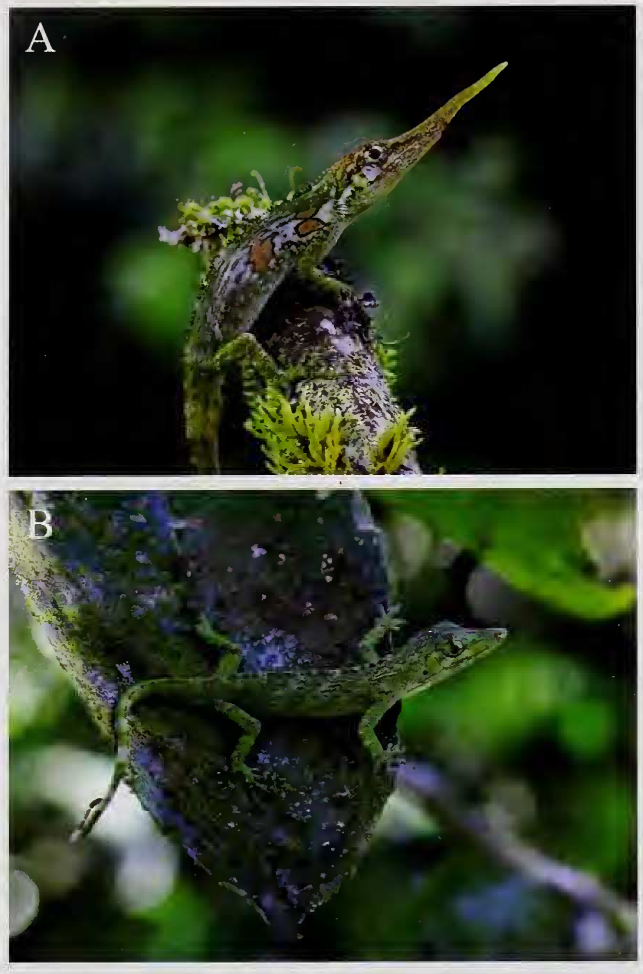

Figure 1. *Anolis proboscis* illustrating sexual dimorphism in rostral horn, coloration, and pattern. Male (A) and female (B).

ecological and morphological diversity of mainland anoles (i.e., the anoles of Central and South America), very few species appear to correspond to the Greater Antillean ecomorphs (Velasco and Herrel, 2007; Pinto *et al.*, 2008; Schaad and Poe, 2010); to the contrary, most mainland species are quite different in ecology or morphology from Greater Antillean ecomorphs (Irschick *et al.*, 1997; Schaad and Poe, 2010). Why mainland and island anoles have taken different evolutionary routes is currently a matter of discussion and research (Velasco and Herrel, 2007; Pinto *et al.*, 2008; Losos, 2009; Schaad and Poe, 2010), but an important first step is establishing the extent to which mainland species correspond to the Greater Antillean ecomorphs. In this respect, *A. proboscis* is particularly interesting, because other than its horn, this species seems to be morphologically very similar to Greater Antillean anoles of the "twig" ecomorph, which are generally cryptically colored, diminutive species with short limbs, narrow heads, and a short, prehensile tail (Fig. 2). Such ecomorphological similarity, however, remains to be formally investigated. Even less well understood is whether the ecology and behavior of this poorly known species corresponds to the twig ecomorph category; in other words, whether *A. proboscis* uses narrow surfaces, moves cryptically, and exhibits other twig anole characteristics (Losos, 2009).

Encouraged by recent collections of well over a dozen individuals in the general vicinity of the type locality, we set out to conduct a behavioral and ecological study of *A. proboscis* with the goal of collecting natural history data on this species.

METHODS

We searched for wild individuals of *A. proboscis* in and near Mindo, Ecuador, a town located at 1,275 m on the western slope of the Andes. Upon locating an individual, we quantified characteristics of its microhabitat and observed the behavior of some individuals. We then captured lizards so that we could measure their sprinting performance and morphology and determine their stomach contents. Sample sizes are presented in the data tables.

Morphology

For each individual, we took the following measurements using digital calipers: snout–vent length (SVL), from the tip of the snout to the anterior edge of the cloaca; head length, from the back of the parietal to the tip of the snout; head width, the width at the widest point of the head; head depth, the depth at the

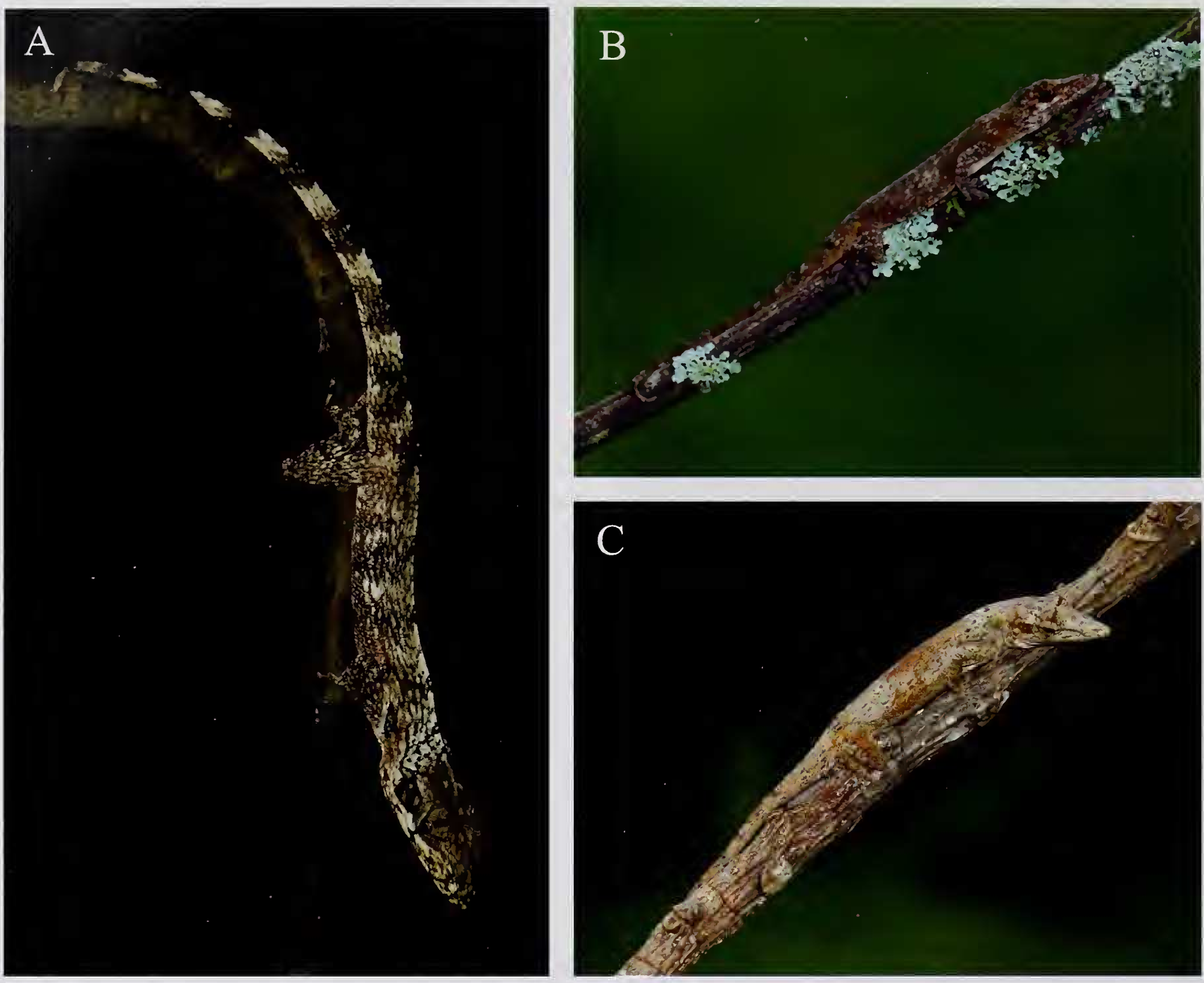

Figure 2. Examples of Greater Antillean twig anoles. *Anolis valencienni*, Jamaica (A); *A. occultus*, Puerto Rico (B); *A. garridoi*, Cuba, (C).

tallest part of the head; lower jaw length, the length of the lower jaw from the back of the retroarticular process to the tip of the lower jaw; jaw out-lever, the distance from the quadrate to the tip of the lower jaw; snout length, the distance from the back of the jugal to the tip of the lower jaw; tail length; femur length; tibia length; metatarsal IV length; and the length, width, and lamella number of the fourth toe on the hindfoot. We measured mass using a portable digital table balance.

All measurements of paired features were taken on the left side of the animal by the same observer. On the basis of these measures, three additional variables were calculated: the in-lever for jaw opening, by subtracting the distance from the quadrate to the tip of the lower jaw from lower jaw length; the in-lever for jaw closing, by subtracting the distance from the jugal to the lower jaw tip from the distance from the quadrate to the lower jaw tip; and hindlimb length, the sum of all hindlimb segments.

All morphological data were $\log_{10}$-transformed before analysis to meet assumptions of normality and homoscedasticity. To test for morphological differences between the sexes, we first conducted a multivariate analysis of covariance (MANCOVA) on all traits with SVL as a covariate and sex as a factor. Additionally, we ran univariate analyses of covariance (ANCOVA) with SVL as covariate on all traits separately. Of our field-captured *A. proboscis*, a single female was substantially larger than the remaining females, which suggests that we captured mostly small individuals of this sex. Therefore, to compare male and female size, we supplemented our SVL data with measurements from preserved specimens collected in the same area a year before our visit (Poe *et al.*, 2012), and compared size using individuals assumed to be adults and excluding those assumed to be juveniles; in addition, we compared size using all individuals.

We explored morphological convergence between *A. proboscis* and West Indian twig anoles using factor analysis. To do so, species means of all morphological variables were calculated for 26 species of *Anolis*, including three species of twig anoles (*A. occultus*, *A. sheplani*, and *A. valencienni*; see Appendix for a list of species); species were chosen to include multiple unrelated species in each ecomorph class (the trunk ecomorph being the exception, in which the two species are closely related). Morphological traits were regressed against SVL and unstandardized residuals were extracted; these residuals and SVL were used as input for a factor analysis with varimax rotation. Factors with eigenvalues greater than one were saved and plotted to determine where *A. proboscis* was situated in multivariate morphological space relative to West Indian twig anoles. Only data for males were used in this analysis to avoid confounding effects of sexual dimorphism.

Sprint performance

To measure sprint performance, we recorded the maximum sprint speeds of recently captured animals in a field laboratory setting. Sprint speeds were calculated by inducing a lizard to run up a 1.5-cm-diameter dowel placed at an angle of 45°. Pairs of photocells, set at 25-cm intervals and connected to a portable computer, recorded the times at which the lizard passed the cells, and we measured the lizard's velocity over each 25-cm interval using a computer software program. Lizards were encouraged to run by tapping the base of the tail. Three trials were conducted for each individual at hourly intervals, and the highest speed recorded over a 25-cm interval was taken as that individual's maximum sprint speed ability. Sprint speeds were measured at temperatures between 22°C and 24°C, corresponding to air temperatures at which we saw the lizards active and to the few body temperature measurements we were able to obtain (below). Only trials in which a lizard appeared to be moving at maximal capacity were retained for analysis. As with the morphological data, we $\log_{10}$-transformed all performance measures before analysis and we tested for performance differences between sexes using MANCOVA and ANCOVA as described above.

To compare the size-corrected sprint speed of *A. proboscis* to West Indian ecomorph species, we calculated the mean sprint speed and SVL of *A. proboscis* and compared that with the sprint speed of 24 other species (the species listed in the Appendix, except *A. conspersus* and *A. maynardi*) after calculating residuals, as described above.

Habitat use and behavior

To quantify habitat use, we conducted visual encounter surveys during the day and at night in a variety of types of habitat, including closed canopy rain forest, disturbed rain forest, roadsides, forest edges, and the planted vegetation within a botanical garden. Walking slowly and using binoculars, we made an effort to thoroughly search all visible vegetation from ground level to approximately 10 m in height. For each anole encountered, we recorded the sex of the animal, the type of substrate upon which it was found, and the height and diameter of the substrate (measured with a measuring tape where possible or estimated for animals high off the ground). One lizard was discovered climbing up a tree trunk, but all others were stationary when first observed.

When possible during the day, we videotaped lizards to determine how much time they spent in activities such as locomotion and displaying. We videotaped most lizards that we discovered during the day, although some behavioral observations were made on animals that were not videotaped. In addition, one night we located five lizards and returned to their sleeping sites shortly before dawn. We then watched the lizards as they began their activites. Air temperature at dawn was cool (14.5°C) and did not appreciably warm until the sun struck the lizards' perches several hours after sunrise. Because lizards were relatively inactive early in the morning (although some displayed and moved to some extent), we only analyzed movement data from after 0900 h. Lizards were videotaped from a horizontal distance of 3–8 m for periods ranging from 21 to 115 min (not including the 3 hours of watching lizards in the morning before they became active). Videotapes were later analyzed and the duration of each movement of the following type was recorded: crawl, walk, run, forage, display. Crawls were distinguished from walks by the speed of the movement and the time it took to move one body length. A crawl was defined as a slow movement that took approximately 7–12 seconds for the lizard to move one body length. A walk was defined as a moderate speed movement forward that took approximately 2–6 seconds to move one body length. Only one lizard was observed running; this was defined as a brisk movement that was substantially faster than any walks (although compared with movements of other anoles, it was not very rapid). Foraging was defined as the time a lizard spent obtaining and consuming prey. Displaying was defined as a dewlap extension or head bob. Only one individual was observed head bobbing and no individuals were observed doing push-ups, a display movement that is common in many other anole species. One lizard did not move during the period it was observed; data for that individual are not included in the analyses because of the possibility that the lizard's inactivity was due to our presence, in accord with previous studies (e.g., Johnson *et al.*, 2008).[1]

After recording behavioral and habitat data, we captured lizards when possible to collect data on morphology, performance, and diet. For two lizards that we caught during the day without disturbing them greatly in the capture process, we measured body temperature using a quick-reading cloacal thermometer. We also measured the air temperature at the time and site of capture using the same thermometer.

Diet

Lizards were stomach-flushed shortly after capture using a water-filled syringe with an attached feeding needle (a ball-tipped steel needle). First, we selected a syringe and needle of appropriate size for the animal at hand. A small plastic ring was then inserted

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[1] This protocol was adopted because anoles disturbed by observers often become inactive (for an extreme example, see Losos *et al.* [1991]). That the lack of movement is related to the observer's presence is often indicated because the lizard looks directly at the observer and is attentive to small movements. Including such data would risk biasing interspecific comparisons toward the finding that species that are more sensitive to the presence of observers move less. The alternative—that the presence of observers causes lizards to move more frequently—seems unlikely, except in those cases in which the lizard immediately flees.

Table 1. Comparison of *Anolis proboscis* to *Anolis* ecomorphs. Values are means ± 1 SD for ecomorph classes. The effect of size removed by calculation of residuals. Species sample size in parentheses. Forelimb measurements only taken on some species, indicated by second number in parentheses. Toepad width and lamella number from hindfoot; values for forefoot qualitatively identical.

	Crown-Giant (4, 1)	Grass-Bush (4, 2)	Trunk (2, 2)	Trunk-Crown (8, 4)	Trunk-Ground (5, 1)	Twig (3, 1)	*A. proboscis*
Head height	0.02 ± 0.03	0.03 ± 0.05	0.02 ± 0.00	−0.02 ± 0.04	0.03 ± 0.06	−0.03 ± 0.00	−0.01
Head width	0.00 ± 0.02	−0.01 ± 0.05	0.06 ± 0.01	0.01 ± 0.04	0.03 ± 0.05	−0.08 ± 0.03	−0.09
Head length	0.00 ± 0.02	0.01 ± 0.03	−0.02 ± 0.02	−0.00 ± 0.02	0.00 ± 0.04	−0.01 ± 0.01	−0.00
Forelimb length	−0.05	−0.03 ± 0.02	0.12 ± 0.00	0.00 ± 0.03	0.07	−0.20	−0.04
Hindlimb length	−0.00 ± 0.06	0.07 ± 0.04	0.05 ± 0.03	−0.00 ± 0.05	0.07 ± 0.03	−0.17 ± 0.07	−0.14
Tail length	0.01 ± 0.08	0.18 ± 0.07	−0.11 ± 0.01	0.01 ± 0.06	−0.01 ± 0.02	−0.18 ± 0.08	−0.08
Mass	−0.02 ± 0.04	−0.01 ± 0.08	0.09 ± 0.04	0.03 ± 0.07	0.08 ± 0.07	−0.17 ± 0.13	−0.18
Sprint speed	−0.09 ± 0.19	0.13 ± 0.25	−0.06 ± 0.04	0.15 ± 0.11	0.18 ± 0.08	−0.40 ± 0.57	−0.54
Toepad width	−0.02 ± 0.07	−0.05 ± 0.06	0.09 ± 0.00	0.04 ± 0.10	−0.01 ± 0.08	−0.06 ± 0.03	0.01
Lamella number	0.01 ± 0.04	−0.01 ± 0.06	−0.02 ± 0.01	0.03 ± 0.07	−0.04 ± 0.03	0.00 ± 0.04	0.00

between the jaws to allow unhindered flow of water and food out of the digestive tract. The needle was inserted gently into the pharynx and pushed further down the digestive tract to the end of the stomach (the position of the needle can easily be detected by palpation). Next, water was injected from the syringe while the stomach of the lizard was massaged. Water was added until the food was regurgitated or pushed out with the water. Stomach contents were placed in individual vials with 70% ethanol and labeled. We flushed the stomachs of all individuals captured with the exception of one male. Prey items were identified at least to Order, and to Family when possible.

RESULTS

Morphology and sprinting performance

We captured 9 males and 11 females. Males (maximum SVL = 83.6 mm) are slightly larger than females (maximum SVL = 76.9 mm), a difference that was marginally nonsignificant when only adult individuals were compared (analysis of variance [ANOVA]: $F_{1,9} = 4.63$; $P = 0.060$), but significant when all individuals were compared (ANOVA: $F_{1,28} = 9.87$; $P = 0.004$; see Supplementary Fig. 1 for additional details). Accounting for size, the sexes do not differ in other morphological traits (MANCOVA, Wilks' $\lambda = 0.04$; $F_{17,1} = 1.41$; $P = 0.59$). Univariate analyses also showed no differences between sexes in morphological traits or sprinting performance with differences in size accounted for (all $P > 0.05$). Horn length increases with SVL of males ($r^2 = 0.87$, $P < 0.001$; slope = 1.78).

Anolis proboscis is a slender lizard with short limbs, a short tail, and a narrow head (Table 1). In all of these respects, morphometric measurements for *A. proboscis* correspond closely to data for West Indian twig anoles. A factor analysis performed on the residual morphometric data for 26 *Anolis* ecomorph species and *A. proboscis* retained four factors jointly explaining 81% of the variation in the data set. The first factor loaded most strongly for hindlimb dimensions, the second for head and jaw length, the third for toepad characteristics, and the fourth for the lever arms of the jaws (Table 2). A plot of the first two factors clearly discriminated between twig anoles and other Caribbean anoles, with twig anoles having proportionally shorter hindlimbs.

TABLE 2. FACTOR ANALYSIS PERFORMED ON MORPHOLOGICAL DATA FOR *ANOLIS PROBOSCIS* AND 26 SPECIES OF CARIBBEAN *ANOLIS* LIZARDS. ALL VARIABLES EXCEPT SNOUT–VENT LENGTH ARE RESIDUALS. BOLD VALUES REPRESENT LOADINGS GREATER THAN 0.7.

	Factor 1	Factor 2	Factor 3	Factor 4
Eigenvalue	5.32	4.11	3.70	2.31
% variation explained	27.99	21.63	19.45	12.14
Snout–vent length (mm)	0	0	0	0
Toepad hind width (mm)	0.237	0.003	**0.907**	0.107
Toepad front width (mm)	0.304	0.084	**0.896**	0.013
Lamella number hind	0.129	0.111	**0.759**	0.008
Lamella number front	−0.120	0.013	**0.923**	0.062
Mass (g)	**0.758**	0.051	0.521	−0.064
Tail length (mm)	0.547	0.149	−0.070	0.058
Head length (mm)	0.071	**0.971**	0.002	0.044
Head width (mm)	0.636	0.326	0.548	−0.242
Head height (mm)	0.483	0.500	−0.018	−0.590
Lower jaw length (mm)	0.099	**0.921**	0.095	0.273
Jaw out-lever (mm)	0.022	**0.961**	0.105	0.196
Snout length (mm)	0.009	**0.943**	0.059	0.057
Jaw opening in-lever (mm)	0.044	0.273	0.038	**0.918**
Jaw closing in-lever (mm)	−0.085	0.154	0.073	**0.946**
Femur length (mm)	**0.954**	0.069	0.063	−0.110
Tibia length (mm)	**0.977**	0.026	0.096	−0.050
Metatarsus length (mm)	**0.943**	0.053	0.092	0.085
Length of fourth toe (mm)	**0.922**	0.005	0.107	−0.029

Anolis proboscis falls within this grouping and has similarly short hindlimb dimensions (Fig. 3).

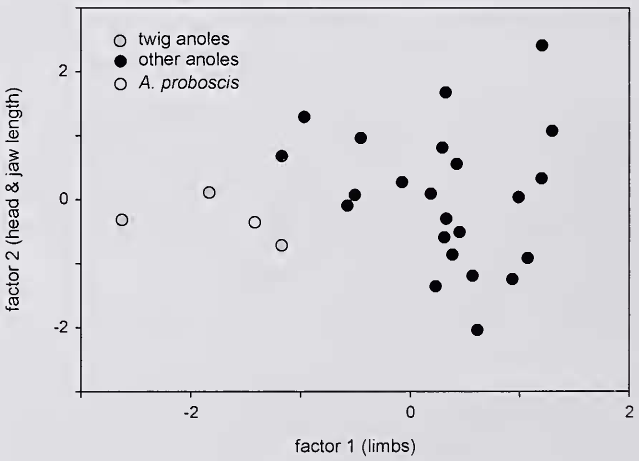

Figure 3. Scatter plot illustrating the position of *Anolis proboscis* in multivariate space compared with Caribbean twig anoles. The first factor is highly correlated with hindlimb length and separates twig anoles (gray circles) from other Caribbean ecomorph species (black circles). Note how *A. proboscis* (open symbol) falls within the cluster of Caribbean twig anoles, indicating that it has similarly short limbs and intermediate head shape for its body size.

Habitat use

We searched a variety of habitats in the area of Mindo, but only located these lizards in disturbed habitats. One location was along the side of a road with sparse vegetation, where the lizards were found on high perches at night. We found individuals at night and during the day at another location, again roadside, but along a botanical garden, where they were found in nonnative bamboo and apple trees. They were also found across the road from the botanical garden, in moderately dense disturbed forest.

Both during the day and at night, lizards were found high off the ground on very narrow perches (Table 3). Of the lizards for

TABLE 3. PERCH USE OF *ANOLIS PROBOSCIS*.

	Height (m ± 1 SD)	Diameter (cm ± 1 SD)
Day		
Male (n = 8*)	4.6 ± 1.1	2.4 ± 3.2
Female (n = 1)	2.5	1.0
Night		
Male (n = 5)	5.9 ± 1.8	1.7 ± 1.9
Female (n = 11)	5.0 ± 1.2	1.9 ± 1.5

*One of these observations probably was of an animal for which data had previously been recorded, so the number of individual males is probably seven.

TABLE 4. TIME BUDGET OF 10 ADULT MALE *ANOLIS PROBOSCIS*. VALUES ARE THE PERCENTAGE OF TIME SPENT IN EACH TYPE OF BEHAVIOR.

	Mean ± 1 SD	Range
Crawl	15.5 ± 21.9	2.5–75.4
Walk	0.9 ± 1.5	0.0–4.8
Run	0.1 ± 0.3	0.0–0.8
Forage	1.0 ± 2.4	0.0–7.6
Display	0.7 ± 1.1	0.0–3.2

which we have quantitative perch data, six of nine lizards observed during the day were on surfaces of 1 cm in diameter or less, as were 9 of 16 animals found at night (and another on a branch 1.5 cm in diameter). During the day, almost all lizards were found on branches or twigs, except for the one male observed climbing up a 10-cm-diameter trunk (eventually this lizard moved to thin branches high in the tree). At night, six lizards were found on leaves (all with diameters—which we measured as the widest point of the leaf perpendicular to its long axis—greater than 1 cm), one on a vine, and the remaining nine on branches and twigs.

Of the 11 lizards we observed for behavior data, four used leaves, and two of these lizards spent considerable time sitting and crawling on the leaves. Also, two lizards climbed on narrow vines and another walked on a fruit. Other than that, however, these lizards spent all of their time on very narrow branches and twigs.

Behavior

Lizards spent most of their time sitting, but were surprisingly active (at least relative to other anole species), moving more than 16% of the time (summing time spent crawling, walking, and running [Table 4]; for comparisons to other anole species, see Perry, 1999; Irschick, 2000; Cooper, 2005). For all individuals, by far the most common movements were crawls (online video 1). Only one lizard was observed running, and none of the lizards was observed jumping.

Only a few lizards, two males and a female, were observed displaying. One male displayed twice during 2.5 hours of observation. At 1018, he extended his dewlap for 8 seconds, and at 1046, he displayed again for 18 seconds, this time extending the dewlap twice, the second time accompanied by two head bobs. During both displays, the body remained static. Another male was in the vicinity during these displays. In a separate group of lizards, three males were observed together, only one of which displayed for 94 seconds during 53 minutes of observation (online video 2). That individual displayed four times, each time only extending the dewlap once; in two of these displays, the lizard raised and laterally compressed its body and rocked back and forth. In addition, a female observed from 0600 to 1007 spent 334 seconds displaying. Displays included slow dewlap extensions with long extension periods, often with the forequarters raised off the substrate and the body laterally compressed, as well as periods in which the mouth was opened while the dewlap was extended. Often her body remained raised and compressed after the dewlap was retracted.

We observed that males are able to change the orientation of their horns. In trials

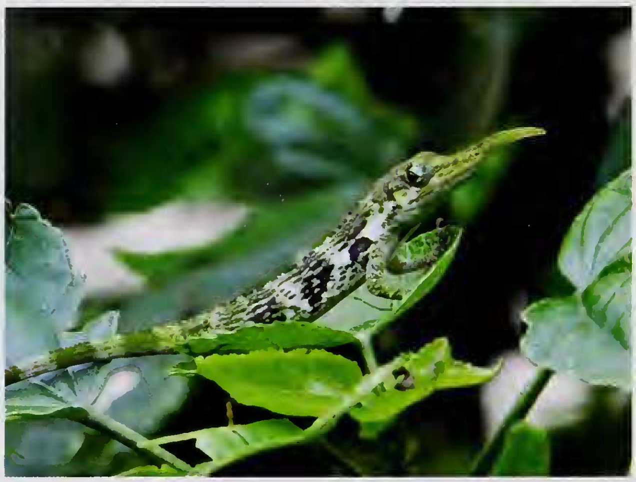

Figure 4. Male *Anolis proboscis*, with horn in a slightly drooped position.

conducted in captivity, we saw one male raise its horn just before capturing a grasshopper (online video 3). In addition, we noted that changes in orientation occurred during observations of wild lizards. These changes did not occur rapidly. Rather, we noticed that the horns of these animals were held in slightly different positions at different times, presumably the result of very slow change. For example, several individuals held the horn completely straight at some times (Fig. 1), but downwardly drooped at others (Fig. 4). In all three males that were videotaped dewlapping, the horn was drooped downward.

Lizards were occasionally seen apparently basking in the sun. We measured body temperatures of two animals at midday of a sunny day. Both animals were in the shade and had temperatures slightly greater than ambient air temperature (23.3°C vs. 22.2°C and 24.4°C vs. 22.7°C).

Diet

Nineteen lizards each contained 4–16 prey items in their stomachs. The most common prey types, both in terms of total number of prey items and number of lizards ingesting that type, were caterpillars, coleopterans, hemipterans, dipterans, and hymenopterans (primarily bees and wasps; Table 5). Few obvious differences existed between the sexes, although 75% of males, but only 45% of females, had consumed beetles, whereas 25% of males, but 55% of females, had consumed dipterans. For the most part, we found little evidence that individual lizards specialized on a particular prey type. Most lizards had consumed a variety of prey items; a male with 10 cicadas in its stomach was one exception (but this individual also had eaten a caterpillar, a beetle, and a hemipteran). In addition to animal prey, six lizards had consumed plant matter, including seeds, flower petals, and small pieces of wood. The number of prey items found in a stomach was not related to sex (ANOVA, $P > 0.65$) or body size (linear regression, $P > 0.25$).

DISCUSSION

In retrospect, it is not surprising that *A. proboscis* went uncollected for nearly 40 years. Cryptic in pattern and coloration, this extremely slow-moving species appears to spend most of its time in dense vegetation high off the ground where it is almost impossible to observe. Indeed, several times when we were watching them with binoculars, lizards were lost due to a slight movement—once as a result of a sneeze, another when the wind blew the vegetation about—and the lizard could not be relocated.

Anolis proboscis is a twig anole

In all respects, *A. proboscis* is extremely similar to Greater Antillean twig anoles. Morphologically, *A. proboscis* has a slender body (as evident by relatively low residual mass), short legs and tail, and a narrow head, all features that characterize twig anoles (Losos, 2009). In addition, both we, Yánez-Muñoz *et al.* (2010), and Poe *et al.*

TABLE 5. DIET OF *ANOLIS PROBOSCIS*.

Phylum	Class	Order	Family*	Number Items (%)	Number Lizards (%)
Gastropoda				1 (0.7)	1 (5.3)
Arthropoda					
	Arachnida				5 (26.3)
		Araneae		7 (4.6)	5 (26.3)
		Pseudoscorpionida		1 (0.7)	1 (5.3)
	Diplopoda			2 (1.3)	2 (10.5)
	Insecta				
		Hemiptera			11 (57.9)
			Cicadellidae	17 (11.2)	7 (36.8)
			Largidae	2 (1.3)	1 (5.3)
			Lygaeidae	1 (0.7)	1 (5.3)
			Reduviidae	1 (0.7)	1 (5.3)
			Tingidae	2 (1.3)	2 (10.5)
			Indeterminate	8 (5.3)	8 (42.1)
		Coleoptera			15 (78.9)
			Anobiidae	1 (0.7)	1 (5.3)
			Carabidae	4 (2.6)	3 (15.8)
			Cetonidae	1 (0.7)	1 (5.3)
			Cucjoidea	1 (0.7)	1 (5.3)
			Curculionidae	5 (3.3)	3 (15.8)
			Dytiscidae (larvae)	7 (4.6)	5 (26.3)
			Histeridae	1 (0.7)	1 (5.3)
			Lycidae	1 (0.7)	1 (5.3)
			Melyridae	1 (0.7)	1 (5.3)
			Scarabeidae	2 (1.3)	2 (10.5)
			Indeterminate	10 (6.6)	8 (42.1)
			Indeterminate larvae	2 (1.3)	2 (10.5)
		Hymenoptera			12 (63.2)
			Apoidea	10 (6.6)	3 (15.8)
			Chalcidoidea and other wasps	11 (7.2)	8 (42.1)
			Formicidae	11 (7.2)	6 (31.6)
		Lepidoptera			14 (73.7)
			Adult	5 (3.3)	4 (21.1)
			Larvae (caterpillar)	25 (16.4)	13 (68.4)
		Diptera			8 (42.1)
			Cecidomyidae	3 (2.0)	3 (15.8)
			Indeterminate	8 (5.3)	4 (21.1)
			Indeterminate larvae	1 (0.7)	1 (5.3)
Total				152	19

*Several prey items identified only to Superfamily.

(2012) noted that *A. proboscis* has a weakly prehensile tail, as do Greater Antillean twig anoles (e.g., Williams and Rand 1969; Hedges and Thomas, 1989). Although larger than many twig anoles, *A. proboscis* is about the size of the Jamaican and Hispaniolan twig anoles, *A. valencienni* and *A. darlingtoni*.

The extent of sexual dimorphism in *A. proboscis* also corresponds to what is seen in twig anoles, which exhibit relatively little dimorphism both in overall body size (Butler *et al.*, 2000) and in body proportions (Butler and Losos, 2002; Losos *et al.*, 2003). We found that males are slightly larger than females overall and that the sexes did not differ in any other morphometric trait once the effect of size was statistically removed. Of course, the sexes differ in possession of the horn, and also in color and pattern (Fig. 1; Yánez-Muñoz *et al.*, 2010).

Primarily using narrow surfaces, *A. proboscis* conforms to the ecological definition of a twig anole.[2] With regard to behavior, twig anoles are generally relatively active foragers, moving slowly, but frequently over great distances (Webster, 1969; Johnson *et al.*, 2008; Losos, 2009) and in this respect, *A. proboscis* again exhibits many similarities (Perry, 1999; Irschick, 2000; Cooper, 2005). Although active, twig anoles generally move very slowly, rarely running and jumping (Losos, 2009); once more, *A. proboscis* is extreme, only once observed running and never jumping.

Twig anoles are often the most cryptic and difficult to find of the ecomorphs. One aspect of the crypticity of *A. proboscis* that we observed is that it rarely displayed. This is consistent with a general trend among West Indian anoles, in which twig anoles tend to display less than other ecomorphs (although substantial intra-ecomorph variation exists in display frequency; Losos, 2009; Johnson *et al.*, 2010).

The Greater Antillean anole radiation is renowned for the extent of interisland convergence; the same six ecomorph classes have evolved repeatedly and independently on different islands (Losos, 2009). However, most mainland anoles do not correspond to any of the ecomorphs, with a few exceptions, such as *A. auratus*, which is clearly a grass anole in both morphology and habitat use (Irschick *et al.*, 1997; Losos, 2009; Schaad and Poe, 2010).

Our results demonstrate not only that *A. proboscis* is a bona fide member of the twig anole class, but they also reaffirm that twig anoles have evolved multiple times on the mainland. Members of the *pentaprion* species group from Central America, distantly related to *A. proboscis*, appear on morphological, ecological, and behavioral grounds to be twig anoles (Losos, 2009; Herrel *et al.*, unpublished observations). Species in the Phenacosaurus clade (formerly considered its own genus) also appear on morphological grounds to be twig anoles (Losos, 2009; Schaad and Poe, 2010), although it is possible that the similarity of these anoles to *A. proboscis* is the result of common ancestry rather than convergence (see below).

The enigma of the horn

Sexual dimorphism may evolve in response to different functional demands imposed on the sexes (e.g., costs of egg bearing in females), to facilitate intersexual niche partitioning, or as a result of sexual selection (Andersson, 1994; Butler *et al.*, 2000). Although one could imagine fanciful functional or ecological purposes for the horn (perhaps the horn is used as a lure to tempt certain types of insects, or allows male horned anoles to warm more rapidly in the morning), it seems unlikely that the horn evolved for any such reasons. Consequently, the most likely explanation, suggested by Williams (1979), is that the horn evolved as a result of sexual selection, either as a way for males to assert dominance over one another or in response to females preferring to mate with larger-horned males. Unfortunately, although we did observe several displays and several males in proximity to each other, we did not discern how the horn might be used in courtship or territorial encounters.

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[2] There is a misconception among some biologists that Caribbean twig anoles are found exclusively on narrow surfaces. However, all Caribbean ecomorph species exhibit variation in where they can be found—at the extreme, just about any species can be found anywhere at least once in a while (Losos, 2009). The differences in habitat use among the ecomorphs refer to where each ecomorph is *usually* found. Twig anoles are usually found on narrow surfaces, but not always (e.g., Irschick and Losos, 1999, fig. 3). In this respect, our finding that *A. proboscis* is found the vast majority of the time on narrow surfaces is congruent with observations on Caribbean twig anoles. Moreover, the occasional twig anole that occurs on a broad surface—such as the one individual *A. proboscis* found on a 10-cm trunk—can lead to an inflated mean value. In fact, the mean perch diameter for *A. proboscis* is substantially smaller than that for the similar-sized Caribbean twig anole, *A. valencienni* (Losos, 2009, fig. 3.14).

We can, however, discount one possibility. In some species of lizards, such as some chameleons, in which males have horns or similar structures, the males use them as weapons in intrasexual combat. However, the horn of *A. proboscis* is an extremely flexible structure, and we observed that it bends when it comes into contact, even gently, with other objects (online video 4). Hence, it seems impossible that the horn could be used as an effective weapon in physical combat. This is supported by observations made when two males were placed on the same branch (Poe *et al.*, 2012): the dominant male flourished its horn and lightly touched the submissive male with it, but did not use it as a weapon.

Why, then, did the horn evolve? One possibility is that it simply evolved as a way to make a male look larger. Many aspects of the displays of male anoles, and of males of other species of lizard, serve to make individuals look larger, such as ventrolateral flattening of the body, erection of crests on the neck and back, engorgement of the throat, and extension of the dewlap (Jenssen, 1977; Losos, 2009). In addition, during aggressive displays to other males, several species of anole will turn sideways, straighten their bodies, and extend their tongues far out of their mouths, perhaps to maximize their apparent body length (Schwenk and Mayer, 1991). In general, larger males have a big advantage in male–male combat (e.g., Rand, 1967; Jenssen *et al.*, 2005; reviewed in Losos, 2009), so any characteristic that makes one male look larger than another may be useful. Alternatively, females may have evolved a preference for males with a horn, perhaps because it made those males look larger, or perhaps for other reasons. A number of chameleon species possess soft rostral projections in lieu of bony horns (e.g., *Rhampholeon spinosus*, *Kinyongia tenue*), as do a number of agamid lizards in the genera *Lyriocephalus* and *Ceratophora* (Schulte *et al.*, 2002), but the horns in these lizards are equally poorly understood. In all of these taxa, species exhibit sexual dimorphism in horn size, shape, number, or presence, and some *Ceratophora* have been described moving their horns in a similar manner to what we observed in *A. proboscis* (described below; Rand, 1961; Schulte *et al.*, 2002). In future studies, comparing the function and evolution of these similar appendages in such distantly related arboreal lizards could prove interesting.

The dewlap of *A. proboscis* is not particularly large (Fig. 5). This small size may have several explanations. Certainly, the dewlap of *A. proboscis* is smaller than those of the three other species with which it is sympatric (Fig. 5). The small size of the dewlap of *A. proboscis* thus may serve as a species-recognition cue, a means for lizards to distinguish conspecifics from sympatric heterospecifics (Losos and Chu, 1998; Nicholson *et al.*, 2007). Alternatively, anoles with smaller dewlaps (or no dewlaps at all) often have other signals, such as colorful body

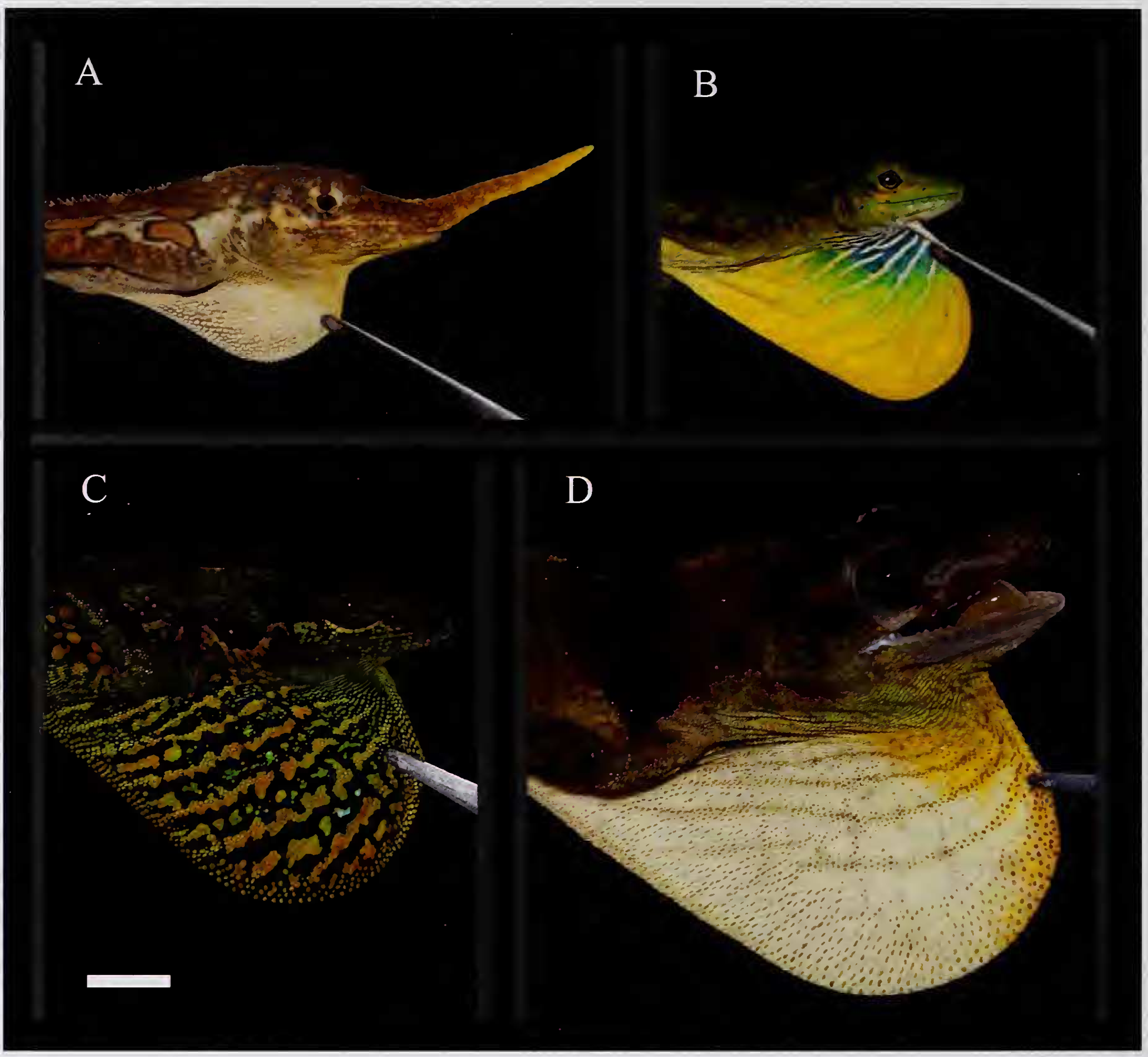

Figure 5. Dewlaps of *Anolis proboscis* (A) and the three anole species with which it is sympatric: *A. gemmosus* (B), *A. aequatorialis* (C), and *A. fraseri* (D). Scale bar (bottom left) equals 1 cm.

patterns or permanently erect crests (Williams and Rand, 1977; Fitch and Henderson, 1987; Losos and Chu, 1998); the presence of a horn may similarly serve as an alternative means of communication. More information on the social behavior of *A. proboscis* is needed before anything more definitive can be said about the function and evolution of the horn.

One final aspect of *A. proboscis*'s horn deserves mention: it is moveable. Our observations concur with those of Poe *et al.* (2012), who observed captive males raising their horns to a 45° angle when approaching food. Poe *et al.* also suggested that males changed the inclination of their horns during social encounters. More generally, we observed that the orientation of the horn changed during the course of behavioral observations; further work is needed to understand the causes and consequences of these adjustments.

Phylogeny

Anolis proboscis and the Amazonian *A. phyllorhinus* have long been considered close relatives, but this is primarily because they both have horns, even though the horns themselves differ somewhat in structure (Williams, 1979). On morphological grounds, Rodrigues *et al.* (2002) consider *A. phyllorhinus* to be closely related to *A. punctatus*, whereas both Yánez-Muñoz *et al.* (2010) and Poe *et al.* (2012) consider *A. proboscis* to be closely related to the Phenacosaurus clade. Phylogenetic analysis indicates that *A. punctatus* and the clade containing *A. proboscis* and the phenacosaurs are not closely related, though both are in the larger Dactyloa clade (Schaad and Poe, 2010; Castañeda and de Queiroz, 2011; Poe *et al.*, 2012). Unfortunately, *A. phyllorhinus* has not yet been included in phylogenetic analyses. In addition, no molecular data have been published for either species of horned anole.

Ecomorphologically, *A. proboscis* and *A. phyllorhinus* are different in many ways. Compared with *A. proboscis*, *A. phyllorhinus* has longer legs, a longer tail, and is green in color. Ecologically, it does not seem to be a twig specialist, as discussed above. Anoles are renowned for their ecomorphological diversity, and comparable differences between closely related anole species are common. Hence, the differences do not strongly argue for distant relationship of the two species; on the other hand, they also do not provide any evidence for a close relationship. If nothing else, these ecomorphological differences suggest that possession of a horn, whether homologous or convergent, is not associated with a particular ecomorphological lifestyle.

CONCLUSIONS

The horned anole of Ecuador is one of the most extraordinary members of a remarkable clade of lizards. Our studies have provided much information about the natural history of this previously unknown species. Nonetheless, the function of the horn remains a mystery. Given the cryptic nature of this species, conducting the requisite detailed studies of social behavior will not be an easy task. Laboratory studies of captive animals, some already ongoing, may prove useful.

More generally, the natural history of mainland anoles, and particularly those of South America, is surprisingly little known. For most species, we know next to nothing about any aspect of their natural history. Such information, of course, is crucial for understanding the evolutionary biodiversity of this group, as well as for conserving it.

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Appendix. Species included in morphometric analyses. Geographic locality and ecomorph class in parentheses. *Anolis carolinensis* and *A. maynardi* are descended from the trunk-crown anoles of Cuba (Glor *et al.*, 2005) and *A. conspersus* is descended from the trunk-crown anoles of Jamaica (Jackman *et al.*, 2002). Ecomorph abbreviations: CG = crown-giant; GB = grass-bush; TC = trunk-crown; TR = trunk; TG = trunk-ground; TW = twig.

A. bahorucoensis (Hispaniola, GB), *A. barahonae* (Hispaniola, CG), *A. brevirostris* (Hispaniola, TR), *A. carolinensis* (Louisiana, TC), *A. coelestinus* (Hispaniola, TC), *A. conspersus* (Grand Cayman, TC), *A. cristatellus* (Puerto Rico, TG), *A. cuvieri* (Puerto Rico, CG), *A. cybotes* (Hispaniola, TG), *A. distichus* (Hispaniola, TR), *A. equestris* (Florida [introduced, native to Cuba], CG), *A. evermanni* (Puerto Rico, TC), *A. garmani* (Jamaica, CG), *A. grahami* (Jamaica, TC), *A. gundlachi* (Puerto Rico, TG), *A. krugi* (Puerto Rico, GB), *A. lineatopus* (Jamaica, TG), *A. maynardi* (Little Cayman, TC), *A. occultus* (Puerto Rico, TW), *A. olssoni* (Hispaniola, GB), *A. pulchellus* (Puerto Rico, GB), *A. sagrei* (Jamaica, TG), *A. sheplani* (Hispaniola, TW), *A. singularis* (Hispaniola, TC), *A. stratulus* (Puerto Rico, TC), and *A. valencienni* (Jamaica, TW).

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